

COMPOSITAE Giseke^{1,2}

Annual, biennial or perennial **herbs** or sometimes **shrubs**, **trees**, or **vines**, variously pubescent or glandular, sometimes glabrous, lactiferous or not; stems terete, sometimes winged or flattened into cladodes. **Leaves** alternate, verticillate, or opposite, sometimes basal, rarely reduced to scales, spines, or wanting, simple or 2- to many-foliolate, entire, or variously toothed, lobed or dissected; petioles present or wanting; the leaf bases sometimes decurrent or clasping; exstipulate, but pseudostipules sometimes present. **Inflorescence** cymose, racemose, paniculate, umbellate, or of solitary capitula, sometimes in indefinite aggregates; usually pedunculate, rarely with the capitula in glomerules (pseudocephalium); often bracteate; usually pedicellate, sometimes bracteolate. **Capitula** with 1-many florets inserted on a receptacle; heterogamous, radiate or disciform, or homogamous, discoid or ligulate; basally enclosed in an involucre; phyllaries (involucral bracts) few to many in 1 to several similar, differentiated, or evenly graded series, free or connate, valvate or imbricate; receptacle convex, concave, flat, or conical; paleae flat or keeled and enfolding the florets, or reduced to hairs or short scales, or wanting; florets epigynous, either all hermaphrodite and protandrous, or female, male, or neuter (sterile); corollas gamopetalous, tubular, filiform, ligulate or bilabiate, usually 3- to 5-toothed, rarely absent, the stamens 5, rarely 3 or 4, epipetalous, filaments usually free, the anthers mostly oblong, marginally connate, introrse with sterile appendages, basally truncate to tailed, the style branches 2, pubescent, glabrate or glandular, the ovary terete or compound, often with apical nectary. **Fruit** usually an achene (cypsela), rarely baccate or drupaceous, or a utricle formed by fusion of the achene with paleae, bracts or other parts, the pericarp mostly hard; pappus usually present, of bristles, awns, or scales; sometimes with a distinct carpodium.

The Compositae is one of the largest flowering plant families in the world, represented by over 1,400 genera and estimates of between 20,000 and 30,000 species. Only the Orchidaceae is comparable in number with about 750 genera and some 18,000 species. The Compositae is cosmopolitan in distribution, occurring on all continents, except Antarctica. The family is well developed in the New World, with Peru being a center of diversity for several tribes. In Peru, there are over 1,400 species of Compositae representing approximately 10% of the total Peruvian flora (see Gentry, *A Conspectus*).

Presently, 13 tribes are recognized as occurring in Peru. The generic composition of the tribes reflects the results of the Reading Symposium on the Biology and Chemistry of the Compositae (1977).

¹The treatment for the family Compositae is being coordinated by Michael O. Dillon, Field Museum of Natural History, who wrote introductory material including the family description and key to tribes. Tribes are being published separately as they are completed, with authorship indicated at the beginning of the taxon. Each author is solely responsible for his treatment.

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TABLE 3. Estimates of the number of genera and species for the tribes represented in the Compositae of Peru.

Tribe	No. of genera	No. of species
VERNONIEAE	7	39
LIABEAE	12	50
EUPATORIEAE	39	290
ASTEREAE	15	200
INULEAE	10	67
HELIANTHEAE	70	289
TAGETEAE	5	23
ANTHEMIDEAE	6	11
SENECIONEAE	9	231
CALENDULEAE	1	1
CARDUEAE	2	2
MUTISIEAE	21	200
LACTUCEAE	6	29
TOTAL	203	1,432

Estimates of the number of genera and species within each tribe are given in Table 3. The tribes Eupatorieae and Heliantheae are the largest, with each containing some 20% of the total, followed by the Senecioneae (ca. 16%), the Astereae (ca. 14%), and the Mutisieae (ca. 14%). The tribe Liabeae is here recognized and considered most closely aligned with the tribe Vernonieae. The polyphyletic tribe Helenieae (sensu Bentham) is not maintained, with constituent genera being realigned with the tribes Heliantheae, Senecioneae, and Tageteae. The tribe Calenduleae is represented by the introduced ornamental *Calendula officinalis* L. Only the African tribe Arctoteae is unrepresented in the flora.

In Peru, the family has radiated into a wide variety of habitats, including the puna, inter-montane valleys, the lomas of the coastal desert, and the ceja de la montaña; however, few are present in the tropical and subtropical rain forests. Nearly every type of habit is to be found, with perennial herbs and shrubs predominating.

Despite their abundance in the flora, few members of the family have any economic importance in Peru. Several introduced ornamentals are cultivated and sold in the markets (e.g., *Calendula*, *Chrysanthemum*), and some native species are used in folk medicine (e.g., *Spilanthes*, *Tagetes*). At least some members of the genus *Clibadium* and possibly *Ichthyothere* (Heliantheae) are used as fish poison in the lower Amazon basin.

MORPHOLOGY³

Plants of the Compositae display a range of specialized morphology not found in other families, and terminology is often particular to the family. A hand lens or dissecting microscope is useful in examining these plants and some features must be studied with a compound microscope. Literature citations in the following survey of terminology refer mainly to good illustrations of Compositae structures.

Pubescence and glands.—Characteristic hair (trichome) types are found in several groups of Compositae (cf. D'Arcy, 1975; fig. 1). In the Vernonieae hairs are sometimes sturdy, elongate, and single-celled. In the Eupatorieae and Astereae hairs are usually many-celled and uniseriate or moniliform, with the basal or apical cell sometimes slightly differentiated. Arachnoid hairs, too fine to be seen in cellular detail under magnifications less than $\times 45$, occur and may form tomentum in the Inuleae, Liabeae, Senecioneae, and Cardueae. A specialized "verrucose hair" occurs in many genera of the Heliantheae. This hair consists of a multicellular basal rosette, one or two sturdy, distinctly verrucose, erect cells, and an apex of one or two smooth, acicular cells. The basal rosette of cells is sometimes calcified giving the leaf a punctate appearance, and the sometimes calcified rugose and apical cells may result in a scabrous leaf surface. Large multiseriate hairs occurring in *Trixis* (Mutisieae), *Hieracium* (Lactuceae), and *Pectis* (Tageteae), and others may be termed bristles. Branched hairs occur on *Hieracium* and some species of *Senecio*. For a discussion of the double hairs (Zwillingshaare) found on the ovaries of many genera and especially of some primitive elements, see Hess (1938).

Paleae (chaff) and receptacle (torus).—Convention refers to bracts external to the outermost whorl of florets as involucre bracts and those internal to it as paleae. Although artificial, this distinction causes little difficulty. The two structures are homologous with leaves but the paleae are usually considerably more modified. Paleae are best developed in the Heliantheae and Mutisieae but isolated species or genera of the Eupatorieae, Astereae, Liabeae, and Lactuceae and perhaps other tribes also have paleae. In the Heliantheae the paleae frequently enfold the ovary and may be bent over the corolla in bud or occasionally are apically modified into awns or cusps. The paleae of *Eclipta*, *Cirsium* and some Liabeae are narrowed into bristles or awns. In many genera paleae are reduced to hairs or low scales which may persist on the receptacle. In some genera, low hairs or spicules on the receptacle are referred to as paleae although they may consist of enations of the

³Adapted largely from D'Arcy, 1975; pp. 837-843.

receptacle, or remains of carpodia and are not homologous with the bracts noted above. Aged receptacles may be fimbriate (fringed), pilose, foveate (pitted), verrucose (warty or knobby), alveolate (honeycombed), spiculiferous, muricate (spiny), or naked (lacking paleae). The receptacle tissue may be completely sclerified or include parenchyma.

Corollas.—Corollas (Hoffman 1894: 99, 101; Solbrig 1963: 451; Bentham 1873: tab. 8; D'Arcy 1975: figs. 34E, 104, 106, 34B, 48B, 81A, 93B, 98B, 57C, 58C) are considered to be either ligulate (rays) or tubular (disc), although the tubular form includes modifications to campanulate, funnelform, etc., and ligulate corollas usually consist of a tube and a straplike ligule. When extremely narrow, corollas are termed filiform or capillary. The outline made by the top of the corollas and paleae is referred to as the disc. In the Lactuceae all corollas have a 5-lobed ligule. In other groups, ligulate corollas are confined to the outer whorls of florets on the head or are lacking. In the Mutisieae, ligulate corollas have a 3- or 4-lobed ligule and short, opposing lobes at the top of the tube (bilabiate). In the Astereae, Inuleae, Heliantheae, Tageteae, Senecioneae, and Anthemideae, ligules are 2- to 3-lobed or entire, and an opposing lobe is seldom present. In *Zinnia* and *Heliopsis* (Heliantheae) the corolla consists of a ligule persistent on the achene and a tube is lacking, and in *Melampodium* also the tube may be obsolete. Ligulate corollas are lacking in all Peruvian taxa of Vernonieae, Eupatorieae, and Cardueae and only tubular corollas are present. Tubular corollas consist of a basal tube, an expanded limb, and 4-5 apical lobes. They are mostly actinomorphic but sometimes one suture of the limb is deeper than the others (e.g., *Elephantopus* and *Pseudoelephantopus*), and in other cases two sutures are deeper, producing slightly bilabiate corollas. In *Cotula mexicana* (Anthemideae) the disc corollas are regularly 3-lobed, a rarity in the family.

Sexual condition.—Sexual condition of the florets is of great systematic utility. In the Vernonieae, Eupatorieae, and Cardueae (Peru) and in a few genera in other groups, all florets are alike, perfect, and have tubular corollas. Such heads are termed discoid. All florets of the Lactuceae are also perfect and have only ligulate corollas. These heads are termed ligulate. In the above mentioned groups all florets are fertile, producing mostly viable achenes. In most other groups, the outer florets are pistillate, lack stamens, and only rarely produce staminodes. The outer florets may have tubular or ligulate corollas and the heads are termed radiate or disciform depending on whether the ligules are elongate (exceeding the stigmas and pappus) or short and inconspicu-

ous. The ovaries may be fertile or sterile. Variations in the above conditions occur in a few groups. Some Mutisieae have two peripheral whorls of pistillate florets, the outer with ligulate corollas and the inner with tubular corollas. Whorls internal to these have perfect florets with tubular corollas. In a few cultivated plants (e.g., some strains of *Dendranthema* and *Tagetes*) proliferation of pistillate, often abortive, florets with ligulate corollas may supplant normal florets with tubular corollas.

Conspicuous, often pellucid, oil glands of various shapes are arranged characteristically on leaves and involucre in the Tageteae. In *Siegesbeckia* (Heliantheae), *Hieracium*, and *Sonchus* (both Lactuceae), large globose glands are displayed on bristles. In *Baccharis* (Astereae), and *Flourensia* (Heliantheae), a coating of glandular material may make the leaf shiny. With the aid of a lens, punctate glands in the leaf surface or globose glandular materials on the surface may be observed in many species. In the Lactuceae a network of laticifers invisible without special techniques yields copious milky sap.

Leaf arrangement.—In Peru leaves are opposite or rarely verticillate in most Eupatorieae, Tageteae, many Heliantheae, and Liabeae, but are alternate in all other groups. Plants with leaves in basal rosettes belong to groups with usually alternate leaves, but can occur in opposite leaved members (e.g., *Paranephelius*, Liabeae). In plants with opposite leaves, it is not unusual for some leaves and branches in the region of the inflorescence to be alternate.

Inflorescence (Capitulescence).—Capitula (heads) are often grouped into recognizable general inflorescences (capitulescences), i.e., cymes, corymbs, racemes, panicles. A capitulum occurring singly is described as solitary. When capitula are aggregated into a secondary capitulum, it is termed a glomerule (pseudocephalium) or synflorescence (e.g., *Elephantopus*).

Involucral bracts (phyllaries).—These are mostly numerous and in most groups are overlapping in several graded series. Except in the Eupatorieae this is referred to as imbricate, but in the Eupatorieae the terms eximbricate, subimbricate, and imbricate are used to refer to degrees of overlapping. In some species of Tageteae, Senecioneae, Mutisieae, and Lactuceae, the bracts do not overlap but are valvate, touching only at the margins, or they may sometimes be marginally connate for part of their length. A whorl of short bracts at the base of the involucre may be referred to as either subinvolucral bracts or as calyculate bracts. Commonly one or more subinvolucral bracts may be found on the pedicel, sometimes in a different phyllotaxy from the rest

of the plant. In *Elephantopus* and *Pseudelephantopus* (both Veronieae), the involucre bracts are decussate, and in these genera with their heads fused into a common receptacle, a series of subinvolucre bracts forms a pseudoreceptacle around the glomerule.

Stamens.—Stamens (Fig. 1, Hoffmann, 1894: 104; Bentham, 1873: tab. 9; Cabrera, 1974: fig. 52, 53; D'Arcy 1975: fig. 1) are usually of the same number as the corolla lobes. Filaments are usually compressed and the anthers are connate or coherent into a narrow tube. The anther apex is usually sterile and differentiated into a distinct, hyaline appendage. In *Ophryosporus* and *Adenostemma* (Eupatorieae) and in *Eclipta* and *Eleutheranthera* (both Heliantheae), the appendage is much reduced or wanting. In the Mutisieae the anther apex is sterile but not demarcated on the dorsal (outer) side, appearing as a homogeneous continuation of the thecae. Anther bases may be blunt, auriculate, sagittate, or with variously elaborated tails. The auricles of adjacent anthers are sometimes united. In some cases short auricles appear to be derived from longer but crumpled tails. Tails are present in most taxa of Inuleae and Mutisieae.

A ring or region of specialized cells near the top to the filaments, the anther collar, acts as a hinge to permit straightening of the filaments at anthesis when the style pushes through the anther tube with much of the pollen. Characteristics of the anther collar have been used systematically in the Eupatorieae and Senecioneae. Endothelial cells of the anthers, visible under a compound microscope after special preparation, have also been of systematic use in the Eupatorieae (King & Robinson, 1970).

Styles.—The style (Hoffmann, 1894: 107, 109; Bentham, 1873: tab. 10; Solbrig, 1963: 443; Cabrera, 1974: 54-56; D'Arcy, 1975: fig. 1) is typically a 2-branched shaft which may have an expansion (node) near the base. The basal expansion sometimes is stipitate above the ovary by a slender pedicel. The base of the shaft is frequently immersed in a cupular nectary on the ovary apex. In some species the branches do not separate and the shaft is entire. In most cases the dorsal (abaxial) surface is pubescent and the ventral (adaxial) surface is more or less flat. The stigmatic region is on the edge or ventral surface in a configuration characteristic of the tribe. Not always correlated with stigmatic position, several shapes of style branch are common:

Lactuoid: Branches slender, longitudinally uniform, and sparingly pubescent. The apex is acute or obtuse. This type occurs in the Lactuceae and in pistillate florets of other tribes.

Vernonioid: Branches elongate, longitudinally uniform, and often copiously pubescent. This type occurs in the Vernonieae and Liabeae.

Eupatorioid: Branches elongate, gradually expanded near the apex, minutely pubescent, papillose, or smooth. It is stigmatic at the margins near the base, and distal portions of the branches may be referred to as appendages. This type occurs in only the Eupatorieae.

Senecioid: Branches often short, truncate, the apex with a fringe of papillae or hairs (penicillate). This type occurs in some species of Senecioneae, Anthemideae, and Inuleae.

Helianthoid: Branches are short, pilose near the apex, and sometimes with a triangular or filiform appendage at the tip. This type occurs in several genera of Astereae, Inuleae, and Heliantheae, and intergrades with the Senecioid type.

Carduoid: Branches short and smooth, the shaft has an annulus of hairs or thickening near the apex. This type occurs in the Cardueae.

Ovaries.—Taxonomic characters of the ovary are usually expressed in terms of the achene, and younger stages may be misleading. Wings in some *Verbesina* (Heliantheae) species do not develop until after anthesis, while in *Wulffia* (Heliantheae) the awn (pappus) is deciduous soon after anthesis. In many groups a copular nectary is present at the apex of the ovary and in some genera, e.g., *Ayapana* (Eupatorieae), it is conspicuous. This is distinct from the expanded style base which resembles a nectary in some groups. The nectary may be stipitate. It may envelop the basal enlargement of the style shaft or end below it, in which case the stylar expansion appears stipitate. The nectary and style shaft are adnate only at the base. In several tribes—Vernonieae, Eupatorieae, Inuleae, Tageteae, Liabeae, and Anthemideae—the ovaries are characteristically terete, often ribbed, while in the Astereae and Heliantheae they are often compressed laterally (radially) or dorsiventrally (tangentially).

Fruits (achenes).—The usual dispersal unit in the Compositae is the achene, which consists of pericarp, endosperm and embryo, and sometimes includes a pappus, persistent nectary, and carpodium. The pericarp (rind) is usually hard but is soft and fleshy in *Wulffia*. The exocarp is sometimes transparent. The achene may be apically narrowed into a beak which subtends the pappus, and the top of the beak may be expanded in a flange. All structures surmounting the achene except the nectary are referred to as pappus. This may consist of hairs, bristles, scales (squamellae), awns or rarely glands, and sometimes these elements are fused in a corona or annulus. Bristles or hairs are

usually strigulose (barbellate, scabrid) and are especially fine and numerous in the Senecioneae and Lactuceae. Stout bristles are sometimes basally flattened or expanded. Scales may be lacerate. In the Heliantheae awns are common. While the pappus is of great utility in identifying Compositae, it is not unusual to find epappose (calvous) achenes in individuals or species of normally pappose groups (e.g., *Galinsoga*). The carpopodium (hypophysis) is sometimes conspicuous, and the cellular arrangement has been given taxonomic weight in the Eupatorieae. A stipe arising above the carpopodium occurs in some species of *Verbesina*.

Frequently, the achene is united with enveloping bracts or paleae or with adjacent florets, and the compound structure falls together. This compound fruit may be termed a utricle in the same sense as the term is used in the Chenopodiaceae and Urticaceae. It has also been known as an involucre fruit or fruiting involucre. The utricle may be flat and winglike or samaroid as in *Delila*, covered with hooks or spines and burlike as in *Acanthospermum*, or the bract may be tightly fused to and hardly distinguishable from the achene as in *Melampodium* (all Heliantheae). Several achenes (or heads) may be held in glomerules with associated bracts to form a burlike utricle in members of the Vernoniaceae.

In a number of Peruvian Compositae the fruit is fleshy and bird-dispersed. The inulin-rich pericarp of *Wulffia* is soft and fleshy and this baccate fruit is technically a drupe. In *Clibadium* and *Milleria* (both Heliantheae) parts of the involucre are fleshy or even juicy and form a baccate structure. The baccate condition is best noted in fresh material and may pass unnoticed when dry.

Achene shape is sometimes indicative of tribe; thus, the Heliantheae and Cardueae have generally larger achenes than those of other tribes, and in the Lactuceae, Tageteae, and Mutisieae, fruits are often long and thin. Achenes are often compressed in the Astereae and Heliantheae and sometimes in the Lactuceae, but are mostly oblong and cylindrical in the Vernoniaceae, Liabeae, Eupatorieae, Inuleae, and Senecioneae. Winged achenes occur in the Heliantheae and Anthemideae.

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KEY TO TRIBES OF PERUVIAN COMPOSITAE⁴

1. Heads with staminate or perfect florets towards the middle, the corollas tubular or bilabiate; sometimes with pistillate florets towards the outside; usually sap not milky.
 2. Anther tips with sterile, tongue-like, often hyaline appendages.
 3. Florets all alike, perfect, corollas tubular, not yellow; anthers not tailed; receptacle usually naked.
 4. Leaves alternate; style branches slender, terete, hairy all over, the style shaft apically hairy; anthers auricled (tailed in *Piptocarpha*); hairs often 1-celledTribe VERNONIEAE
 - 4'. Leaves mostly opposite (except sometimes in the region of inflorescence); style branches gradually expanded near the tips, papillose or short-hairy, the shaft often glabrous; anthers obtuse or rounded; hairs multicellular, often moniliformTribe EUPATORIEAE
 - 3'. Florets often not all alike, corollas often yellow; anthers sometimes tailed; receptacle naked or with paleae.
 5. Leaves mostly not spiny; involucre bracts not spiny; anthers tailed or not; style shaft without an apical ring.
 6. Leaves alternate; style branches flattened-fusiform, sometimes apically appendaged or rounded; anthers tailed or not; receptacle mostly naked; pappus mostly bristles.
 7. Anthers obtuse; style branches often appendaged; achene often compressed; hairs multicellularTribe ASTEREAE
 - 7'. Anthers tailed; style branches rounded; achene plump; hairs arachnoidTribe INULEAE
 - 6'. Leaves alternate or opposite; style branches flattened-fusiform, sometimes apically appendaged; anthers not tailed; receptacle with paleae or naked; pappus of bristles, awns or scales.

⁴Adapted in part from D'Arcy (1975).

8. Pappus of awns, bristles or scales; style branches often appendaged.
9. Involucre without transparent margins; leaves mostly opposite, often 3-nerved from base or trifoliolate.
10. Receptacle naked; involucre bracts equal, mostly valvate (biseriate in *Schizothrichia*), with pronounced pellucid glands; leaves glabrous to puberulent, typically bearing conspicuous pellucid secretory cavities or glands filled with strongly scented essential oils
Tribe TAGETEAE
- 10'. Receptacle with paleae, squamellae, bristles or merely deeply alveolate (rarely truly naked); involucre bracts unequal, overlapping, 2- to many-seriate, lacking pellucid glands; leaves variously pubescent or glabrous, pellucid glands absent.
11. Receptacle with costate paleae, enfolding the achenes; achenes usually compressed; pappus of scales, awns, or rarely of numerous, strigose bristles; leaves opposite or alternate, mostly eglandular; hairs often verrucoseTribe HELIANTHEAE
- 11'. Receptacle deeply alveolate, with the margins of the alveolae prolonged into stiff mostly subulate awns, squamellae or bristles, rarely with true paleae (i.e., *Chionopappus*) or naked (i.e., *Cacosmia*, *Philoglossa*); achenes usually cylindrical to turbinate, (2-) 5- to 10-angled; pappus generally biseriate, the inner series of bristles and the outer of bristles or squamellae, rarely absent (i.e., *Cacosmia*); leaves opposite or whorled in a basal rosette, usually tomentose belowTribe LIABEAE
- 9'. Involucre with hyaline, transparent margins; leaves alternate, with strong midrib.
12. Leaves usually dissected, often aromatic; style branches in disc and ray florets truncate, penicillate; pappus paleaceous, coroniform, or absent
Tribe ANTHEMIDEAE
- 12'. Leaves entire, not aromatic; style branches of ray florets filiform, glabrous, and of the disc florets, undivided; pappus lackingTribe CALENDULEAE
- 8'. Pappus of soft, silky, hairlike bristles; style branches not appendagedTribe SENECTIONEAE
- 5'. Leaves and involucre bracts spiny; anthers tailed; style shaft with an apical ringTribe CARDUEAE
- 2'. Anther tips sterile, but not differentiated into hyaline, tongue-like appendages; anthers mostly tailedTribe MUTISIEAE
- 1'. Heads with only perfect florets, the corollas ligulate, 5-denticulate; sap milky
Tribe LACTUCEAE